Journal of the Lepidopterists' Society
63(2), 2009,83-88

SEX BIAS ADULT FEEDING FOR GUMWEED (ASTERACEAE) FLOWER NECTAR AND EXTRAFLORAL RESIN BY A WETLAND POPULATION OF *LYCAENA XANTHOIDES* (BOISDUVAL) (LYCAENIDAE)

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ABSTRACT. With the exception of some tropical genera, most butterflies rely on nectar as the primary adult resource and feed on non-floral resources, like tree sap, opportunistically. We found that an isolated wetland population of *Lycaena xanthoides* (Boisduval) (Lycaenidae) in western Oregon, USA, frequently uses both flower nectar and extra-floral resin of *Grindelia integrifolia* DC. × *G. nana* Nutt. var *nana* (Asteraceae) as an adult food resource. There were sex biases in nectar- versus resin-feeding preferences, with males feeding on *Grindelia* flower nectar more frequently than resin, and females feeding on resin more frequently than nectar. A combination of taste tests and sucrose estimates through a handheld refractometer suggested that the *Grindelia* resin may be a source of sugars, while a Kjeldahl analysis detected organic nitrogen at 2.6 ppm in the resin. We propose that the wetland population of *L. xanthoides* has either evolved or is evolving to use *Grindelia* resin as an adult resource because it is predictable in abundance over the landscape, unlike alternate non-floral adult resources.

Additional key words: nectar preference, *Grindelia*, butterfly behavior, adult butterfly resources, butterfly conservation

In temperate zones worldwide, butterflies typically rely on flower nectar as an adult energy source (Gilbert & Singer 1975; Boggs & Ross 1993; Boggs 1997a; Rusterholz & Erhardt 2000; Tooker *et al.* 2002) while feeding on non-floral resources such as feces, carrion, rotting fruit (Gilbert & Singer 1975), aphid honeydew (Rosenberg 1989; Corke 1999), and tree sap (Rosenberg 1989; Krenn *et al.* 2001; Warren 2005) appears to be largely opportunistic and likely supplemental to the primary diet. In tropical regions, specialization of adult butterflies on non-floral resources, like rotting fruit (DeVries *et al.* 1997; Krenn 2001; Knopp & Krenn 2003; Fischer *et al.* 2004; Molleman *et al.* 2005), is a strategy for acquiring resources infrequently used by temperate butterflies. Consumption of adult butterfly resources can directly influence population demographics by increasing fecundity (Boggs & Ross 1993; Boggs 1997a; Fischer & Fiedler 2001; Fischer *et al.* 2004), contributing to a longer lifespan (Hill & Pierce 1989; Karlsson & Wickman 1990; Fischer & Fiedler 2001), and providing energy for flight (Corbet 2000), which is related to both survival and fitness. Spatial and temporal aggregation of adult resources across a patchily distributed landscape of resources may also concentrate adult butterflies (Wiklund 1977; Peterson 1997; Schneider *et al.* 2003; Auckland *et al.* 2004), increasing opportunities for mating. For butterflies that have obligate associations with one or a few preferred adult resources, the combination of larval and adult resource distribution will determine whether a particular piece of habitat is suitable for colonization and population persistence. In the case of rare species that are of conservation concern, understanding what resources are preferred and the strength of the insect-resource interaction is essential for estimating habitat quality and providing appropriate targets for restoration (Severns *et al.* 2006).

In this paper, we report on the adult feeding behavior of a rare wetland population of *Lycaena xanthoides* (Boisduval) (Lycaenidae) in the Willamette Valley of western Oregon, USA, and its frequent use of an extra-floral herbaceous plant resin. We furthermore provide evidence that butterflies may derive sugars and nitrogen from this abundant, predictable extra-floral adult resource, and that the contribution of plant resin to the adult diet is an important interaction for local conservation planning in this butterfly species.

Materials and Methods

Study species. *Lycaena xanthoides* is a western North America butterfly primarily found in various dry habitats throughout northern Mexico, California, and southern Oregon (Scott 1986). However, two wetland populations of *L. xanthoides* occur in the Sacramento

Valley of central California (Shapiro 1974) and in the southern Willamette Valley of western Oregon (Severns & Villegas 2005). In these wetland populations, *L. xanthoides* females lay eggs that survive seasonal flooding and adults are restricted to the local wetlands (Severns *et al.* 2006; A.M. Shapiro pers. com. 2006). Western Oregon (Willamette Valley) *L. xanthoides* appeared to be historically rare and was presumed extinct until recently rediscovered (Severns & Villegas 2005). The butterfly population remains precariously small, with an estimated 97 total individuals (L90%=70, U90%=215) among three subpopulations (Ramsey & Severns 2008 in press). Immediately following its rediscovery in the Willamette Valley an attempt was made to understand butterfly-environment interactions that would enhance *L. xanthoides* restoration projects. A key interaction identified was that the Willamette Valley wetland population of *L. xanthoides* had a strong preference (> 85%) for flowers of perennial *Grindelia integrifolia* DC. × *G. nana* Nutt. var. *nana* (Asteraceae) plants (hereafter *Grindelia* and see Chambers 1998 for a taxonomic treatment) despite a conspicuous abundance of alternate nectar sources which other co-occurring butterfly species prefer (Severns *et al.* 2006). Although not reported previously (Severns *et al.* 2006), observations of female nectaring were not as common as male nectaring, despite a nearly equal number of males and females observed. Females commonly perched on the buds of *Grindelia*, but it was not noticed until the summer of 2006 that butterflies may use resin secreted by the plant as a food source. Resins secreted by *Grindelia* plants are generally most abundant on the flower heads of the plant, followed by the leaves, and then the stems (Hoffmann & McLaughlin 1986). A combination of dense glandular trichomes and resin canals (Hoffmann *et al.* 1984) produces conspicuous amounts of resin that appear on flower buds as either a white, sticky, viscous liquid, or a covering of clear, less viscous resin coating the phyllaries (Fig. 1). The clear, less viscous liquid appears while the glands are actively secreting resin, and as the resin dehydrates it becomes more viscous and sticky. *Grindelia* in western Oregon secretes resins beginning before the flower heads open and continues through the end of flower anthesis. *Grindelia* typically has 20 to 40 heads on a flowering plant but particularly large plants can have hundreds of flower heads. Each head has 20–50 disc flowers and 10–35 ray flowers that are open throughout the months of July, August, and September. Since the flight of *L. xanthoides* and *Grindelia* anthesis coincide, the abundance of flowering *Grindelia* plants is unlikely to be limiting in the study populations as flower heads easily number in the thousands.

Feeding observations and analysis. We were careful to record feeding on nectar or resin only if the proboscis was extended either into an open *Grindelia* disc flower or resin on the phyllaries of the inflorescence head. We recorded as many nectaring observations for each individual as possible. Because the study population of *L. xanthoides* is small, it was relatively easy to find identifying wing characteristics (e.g. wing tears, maculation differences, size, wing wear patterns, etc.) for individuals to be accurately followed. To avoid resampling of individuals, nectaring observations were gathered on two different occasions separated by 12 days. On both observation dates, male and female butterflies were encountered and at least 10% of the *Grindelia* heads contained open disc flowers.

We pooled the data within an individual to generate the per individual ratio of feeding on *Grindelia* resin or flower nectar (i.e. the number of flower nectaring observations for individual #1/ total number of feeding observations for individual #1). Ratios of nectar to resin feeding by individual were analyzed for adult resource feeding differences between sexes using a proportions test (Ramsey & Schafer 2002). We used a one-sided Wilcoxon signed-rank test to determine if within sex choice of food resource could be explained by random chance. We chose a non-parametric statistical test because data were not normally distributed and no other transformations (other than a rank transformation) improved the data distribution. Statistical analyses were performed using S-PLUS 6.1 for Windows Professional Edition (Insightful Corp 2002).

Simple sugar and nitrogen resin analysis. We gathered *Grindelia* flower buds from the field during the flight period of L. xanthoides, placed the buds in a

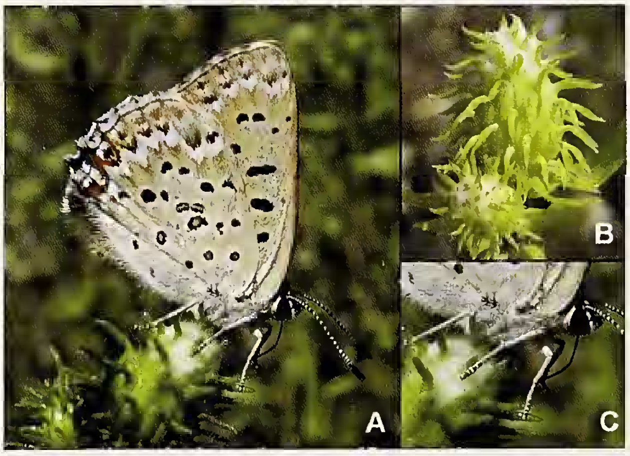

FIG. 1. **A**). Female *Lycaena xanthoides* feeding on *Grindelia* resin, **B**) a *Grindelia* bud covered with resin, and **C**) magnification of the proboscis placement from 1A.

plastic bag on ice, and transported the buds to a laboratory where the resin was extracted. We extracted resin by gently squeezing the phyllaries until a small droplet of resin, approximately 2-8 μL per head, was collected with a micropipette and placed into a centrifuge tube. Approximately 400 μL of exudate were collected from 50 unopened flower heads. The Brix concentration, an index of sucrose concentration, was estimated by taking the mean of five replicates (20 μL/sample) of pooled resin using an Atago ATC-1E handheld refractometer under manufacturer recommended conditions. Total inorganic and organic nitrogen (TKN) was estimated from 50 μL of pooled resin exudate by an acid Kjeldahl digestion (Strickland & Parsons 1972) which measures the amount of organic N in a given sample, excluding nitrites and nitrates (D'Elia *et al.* 1977).

RESULTS

Twenty individuals were reliably followed and the mean number of feeding observations per individual was 4.6 occasions (± 0.72 S.E.). A proportions test indicated that male *L. xanthoides* used flower nectar more frequently than females, while females fed on *Grindelia* resin more commonly than males (Fig. 2). Among the twelve males observed, most of the individuals preferred to forage on flower nectar and small number preferred resin (Fig. 2). Among the eight females observed, most preferred to feed on *Grindelia* resin instead of flower nectar (Fig. 2). No other butterfly species were observed feeding on *Grindelia* resin during the course of this study.

Chemical analyses of *Grindelia* resin suggest that there was a small amount of available resources for adult *L. xanthoides*. The Brix concentration was ca. 2.5% (± 0.3% SEM), suggesting that simple sugars, primarily sucrose, was an available resource in the resin (for a Brix scale comparison, a ripened banana has a Brix measurement between 10 and 12%). Total Kjeldahl nitrogen was 2.16 mg N/L of *Grindelia* resin, indicating that a small amount of organically bound nitrogen may be available for butterfly use.

DISCUSSION

Both sexes of Willamette Valley *L. xanthoides* fed on extra-floral *Grindelia* plant resin as well as flower nectar, and resin appears to have both simple sugars and a small amount of organically bound nitrogen available for use. The sugars are concentrated enough to be tasted by the human tongue (Severns pers. obs.) and the amount of organically bound nitrogen is positioned at the lowest end of ranges documented to support insect larvae (Mattson 1980). Although the observation number is

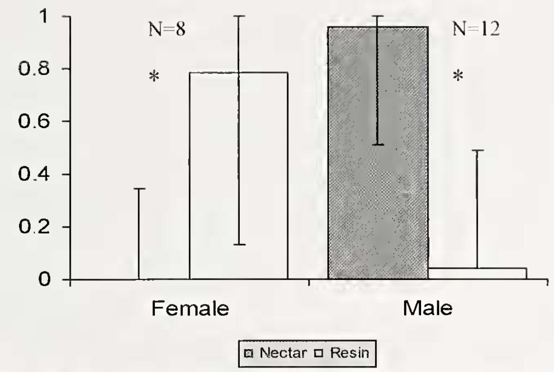

FIG. 2. Bar graph of median resin and flower nectar feeding with error bars representing the 1st and 3rd quartiles. A proportions test indicated that there was a difference in adult resource choice between male and female *L. xanthoides* (Z = -5.093, p = 0.000000176). The percentage of resin and flower nectar feeding instances indicates that females selected resin over nectar (Wilcoxon signed rank test: H0 = number of nectar visits < number of resin visits, Z = 2.446, p = 0.0072), while males preferred nectar over resin (Wilcoxon signed rank test: H0 = number of resin visits < number of nectar visits, Z = -2.2713, p-value: 0.0116). * = statistically significant difference between medians.

small, our data suggest that female Willamette Valley *L. xanthoides* preferred to feed on plant resin over *Grindelia* flower nectar, while males appeared to choose flower nectar over plant resin (Fig. 2). Rusterholz & Erhardt (2000) suggested that, within a species, male and female butterflies prefer different nectar species despite having the opportunity to feed from the same array of flowers. In some instances, sex-specific differences for nectar resources was linked to the availability of amino acids (Alm *et al.* 1990; Mevi-Schüutz & Erhardt 2002, 2003), which females may use to increase their fecundity (Murphy *et al.* 1983; Boggs 1997b). We do not know if any amino acids are available in *Grindelia* resin, but it does appear that soluble nitrogenous compounds are present in the resin, at low concentrations (*ca.* 2.16 mg/L of resin). *Grindelia* resin may also contain a low concentration of sugars as the solution tasted sweet and the Brix concentration of the resin was approximately 2.5%. Handheld refractometers, like the one used in this study, are known to measure compounds other than sucrose and do not measure other disaccharides and most simple sugars (Corbet 2003). Our Brix estimate of sugars in *Grindelia* resin may be an overestimate of some sugars but is also likely to underestimate others. A more rigorous chemical analysis is needed to understand the quantity and diversity of carbohydrate and nitrogen resources available for butterfly use in *Grindelia* resin and flower nectar.

Perhaps the most interesting aspect of *L. xanthoides* use of *Grindelia* resin as an adult resource is that the resins produced by *Grindelia* species are known to contain chemical deterrents effective against lepidopteran larvae (Glendinning *et al.* 1998). It is unclear which compounds within the resin protect *Grindelia* plants from herbivory, but it may be due to grindelic acid (e.g. Mahmoud *et al.* 2000), a diterpene that is similar in structure to diterpenes found in trees of the Pinaceae (Langenheim 2003). This suggests the possibility that females may use secondary plant compounds to provision progeny with chemical predator deterrents. Since female *L. xanthoides* appeared to prefer resin over flower nectar while males displayed an opposite trend under the same environmental and site conditions (Fig. 2), gender associated resource selection may be due to chemical resources that are present or more plentiful in resin that are not in *Grindelia* nectar.

To our knowledge this is the only lycaenid population in temperate zones that has been documented to consistently use plant resin as an adult resource. Nymphalid butterflies in temperate zones do use tree resin opportunistically as an adult resource (Tolman & Lewington 1997; Scott 1986; Layberry *et al.* 1998; Corke 1999; Ômura & Honda 2003), but tree sap is not likely a dependable enough resource to annually support a butterfly population. For example, Rosenberg (1989) found that *Limenitis weidemeyerii* Edwards (Nymphalidae), *Vanessa atalanta* (L.) (Nymphalidae), and *Nymphalis antiopa* (L.) (Nymphalidae) fed on willow (Salix) tree sap from wounds created by yellow-bellied sapsuckers, *Sphyrapicus varius* (L.) (Picidae). For tree sap to be a dependable resource for butterflies, birds must be present annually, and tree wounding must be frequent and substantial enough for sap to be available throughout the butterflies' adult life span. In comparison to fruit production by tropical trees and resin production by *Grindelia* plants, the sap available from a wounded tree is a more unpredictable and limited resource. Willamette Valley *L. xanthoides* may be evolving a preference for *Grindelia* resin because it is a predictable, abundant resource in the remnant wetland prairies of western Oregon. Furthermore, this relationship between *Grindelia* resin and *L. xanthoides* may be more geographically widespread. *Lycaena xanthoides* in central California appear to prefer *Grindelia* flowers (Scott & Opler 1975; Shapiro & Manolis 2007) and may even be selective when given a choice of *Grindelia* species (Shapiro & Manolis 2007), but these authors did not note resin feeding. Other butterflies in the Willamette Valley either do not nectar on *Grindelia* flowers, or the species that do visit *Grindelia* flowers do not feed on resin (Severns pers. obs.). These observations suggest that *L. xanthoides* is the only local butterfly species using resin as a primary adult resource. However, it is possible that other temperate butterflies may use *Grindelia* resin as a food resource because members of this genus are common throughout western North America and arid areas of South America (Steyermark 1937), and at least one species is currently under cultivation for resin production in arid regions of North and South America (Timmermann & Hoffmann 1985; Zavala & Ravetta 2001). *Grindelia* species, with a broad geographic range, a predictable extra-floral resin resource, and relatively high local abundance may be a significant non-nectar adult resource for other Lepidoptera.

The Willamette Valley population of *L. xanthoides* is a target species for wetland conservation, in part due to its rarity and local wetland endemism (Severns & Villegas 2005; Severns *et al.* 2006). It was recently argued that there was an important association between the flower nectar of *Grindelia* and the distribution and habitat preference of adult butterflies (Severns *et al.* 2006). It appears that the importance of *Grindelia* may have been underestimated to the remaining Willamette Valley *L. xanthoides* population. In past studies (Severns & Villegas 2005; Severns *et al.* 2006), individuals that perched on *Grindelia* buds, that were likely feeding on resin, were not recorded doing so. Thus, the local dependence of *L. xanthoides* on *Grindelia* resources was likely underestimated. Since flower nectaring observations in past studies indicated that *L. xanthoides* nectared on *Grindelia* flowers ≈ 90% of the time without accounting for resin feeding, it is likely that interaction between Willamette Valley *L. xanthoides* and *Grindelia* as an adult resource is an obligate association. The natural extension of this information to management of the Willamette Valley *L. xanthoides* is that conservation and restoration of habitat must focus on two obligate butterfly resources – the host plant and *Grindelia* – for conservation projects to have the greatest chance of success.

ACKNOWLEDGEMENTS

We thank E. Bradford for helping gather field nectaring data, two anonymous reviewers for providing helpful comments on this manuscript, and S. Villegas (Eugene, Oregon District, Bureau of Land Management) for support of this project and access to the study site.

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Received for publication 28 December 2007; revised and accepted 16 October 2008.